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Geographical Distribution of Sexual and Apogamous Types of *Dryopteris formosana* and *Dryopteris varia* (Dryopteridaceae) in Taiwan

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Cytological observations of the mitotic chromosomes of *Dryopteris formosana* and *D. varia* (Dryopteridaceae) in Taiwan are reported. Only the triploid apogamous cytotype has been reported from *D. formosana*. This is the first report of a diploid sexual type of *D. formosana*. Counts of spore numbers per sporangium of herbarium specimens to presume the reproductive mode in these two species revealed that both sexual and apogamous types of *D. formosana* and *D. varia* are widely distributed in Taiwan. Although the sexual type of *D. formosana* occurs at relatively lower elevations than the apogamous type, such differentiation between cytotypes was not observed in *D. varia*. It is important to understand diploid sexual types to be able to explain variation in apogamous species, because sexual cytotypes should be the source of the variation observed in apogamous cytotypes.

Key words: apogamy, sexual cytotype, Dryopteridaceae, *Dryopteris formosana*, *Dryopteris varia*, reproductive mode, chromosome number

Dryopteris formosana (Christ) C. Christensen (Dryopteridaceae) occurs in China, Japan, and Taiwan (Iwatsuki 1995, Zhang *et al*. 2013, Knapp 2014) and has been considered to be apogamous. Most previous cytological studies reported it to be an apogamous triploid (Kurita 1967, Hirabayashi 1969, 1974, Tsai 1973). Nakato (1987), however, reported a tetraploid cytotype, although its reproductive mode was unknown. Thus far, a sexual type of *D. formosana* has not been reported.

Similarly, diploid and triploid apogamous types of *Dryopteris varia* (L.) Kuntze, which occurs in eastern Asia, were reported in China and Japan (diploid: Hirabayashi 1966, 1967, 1974; triploid: Gibby 1985, Hirabayashi 1970, Lin *et al*. 2002, 2003, Mitui 1966, 1968, Nakato *et al*. 1995, Weng 1989). Tsai & Shieh (1975, 1985) reported a tetraploid sexual type from Taiwan, but the report is unreliable because no voucher specimen or photos of chromosomes were presented in their report. Ebihara *et al*. (2014) recently reported a diploid sexual type of *D. varia* in two localities in northern Taiwan.

In the present study, we discovered a new diploid sexual type of *Dryopteris formosana* in Taiwan. Moreover, we updated the distribution information of the sexual and apogamous types of *D. formosana* and *D. varia* in Taiwan, mainly by counting the number of spores per sporangium in herbarium specimens of the two species.

Materials and Methods

Plant Materials

Five living plants and three leaf samples of

Dryopteris formosana were collected at three localities, Mt. Alishan and Mt. Chihtan in Taiwan between June 30 and July 2, 2014 (Appendix 1). Cytological observations and analyses of the ploidy level were performed on all five living individuals. Voucher specimens have been deposited in the Makino Herbarium (MAK), Tokyo Metropolitan University and in the herbarium of the Taiwan Forestry Research Institute (TAIF).

To determine the reproductive mode, 42 and 51 sheets of herbarium specimens with indehisced sporangia from approximately 330 and 400 sheets of *Dryopteris formosana* and *D. varia*, respectively, in the herbaria of TAIF and the National Museum of Nature and Science (TNS) were investigated.

Cytological observation and estimation of reproductive mode

To observe mitotic chromosomes, root tips were pretreated with 0.004 M 8-hydroxyquinoline for 7 hrs at approximately 17–20°C. After fixation in ethanol and acetic acid (3:1) for 15–30 min, the root tips were hydrolyzed in 1 N HCl and 45% acetic acid (1:1) at 60°C for 10 min and then squashed in 2% aceto-orcein solution. The chromosomes were observed under a Leica DM2500 microscope and photographed using a Leica Application Suite LAS ver 4.4 digital camera.

To estimate the reproductive mode of each herbarium specimen, the number of spores in each sporangium was counted. We examined at least five sporangia with normal spores from each specimen. We estimated samples with 64 spores to be sexually reproductive; plants with 32 spores per sporangium were estimated it to be apogamous (Manton 1950).

Ploidy analyses

Methods of ploidy analyses using flow cytometry followed Hori *et al.* (2014). To determine ploidy level, the DNA content (2C value) of each nucleus extracted from fresh pinnae was measured using a CyFlow Ploidy Analyzer PA-II (Partec, Munster, Germany) and the CyStain UV Precise P kit (Partec). Approximately 100 mm^2 of a segment of pinna was torn into several pieces and finely chopped with a razor blade into 0.25 mL of nucleus extraction buffer from the kit. Subsequently, 0.8 mL of staining solution from the kit was added to the chopped tissue. The crushed tissue and buffers were filtered through a 30-μm nylon mesh (Partec). Sections of fresh leaf tissue of *Nicotiana tabacum* L. (approximately 25 mm^2) were used as internal standards.

Results

Ploidy and reproductive mode

The mitotic metaphase chromosome number in four individuals of *Dryopteris formosana* (*Hori 1394*, *1409*, *1413*, and *1414*) was $2n = 82$; the number of spores per sporangium in these samples was 64 (Fig. 1a). The base chromosome number of *Dryopteris* is $x = 41$. Accordingly, the plants from which these samples were obtained were determined to be sexual diploids. A photograph and a diagrammatic drawing of one individual (*Hori 1409*) are shown in Fig. 2.

The metaphase chromosome number of the remaining sample (*Hori 1412*) was $2n = 123$ (Fig. 3), and the number of spores was 32 spores per sporangium (Fig. 1b). This sample was determined to be an apogamous triploid.

The DNA content of diploid sexual individuals of *Dryopteris formosana* was 1.31–1.46 times that of the internal standard (*Nicotiana tabacum*) in our ploidy analyses. Considering that the DNA content (2C value) of *N. tabacum* is approximately 11.7 pg (Narayan 1987), the DNA content of *Hori 1394*, *1409*, *1413*, and *1414* was estimated to be approximately 15.4–17.1 pg/nucleus. In contrast, the genome size of the triploid apogamous individual of *D. formosana* was 2.1 times that of the internal standard (*N. tabacum*) and was thus estimated to be 24.9 pg/nucleus.

Reproductive mode of herbarium specimens examined and geographical distribution of the two cytotypes

The number of spores per sporangium was determined from 42 specimens of *Dryopteris formosana.* Among them, 21 specimens had 64

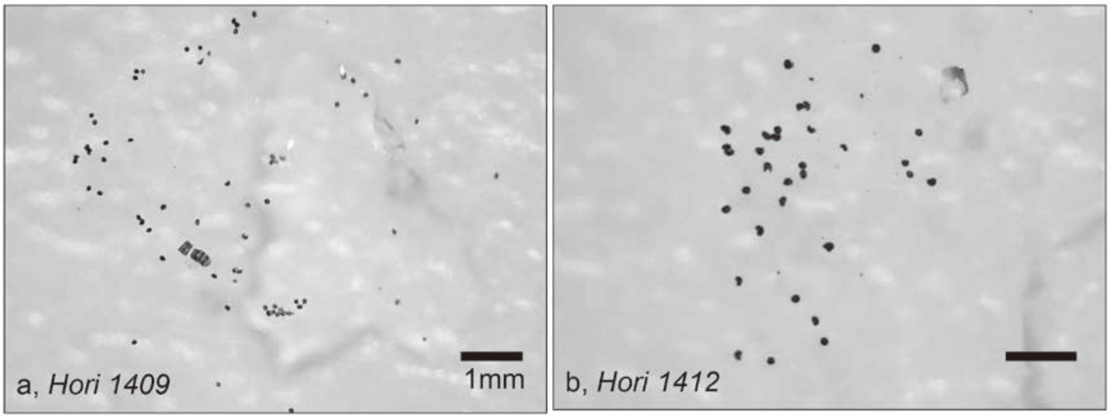


FIG. 1. Photograph of spores in sporangium of diploid sexual (a. *Hori 1409*) and triploid apogamous (b. *Hori 1412*) individuals of *Dryopteris formosana*.

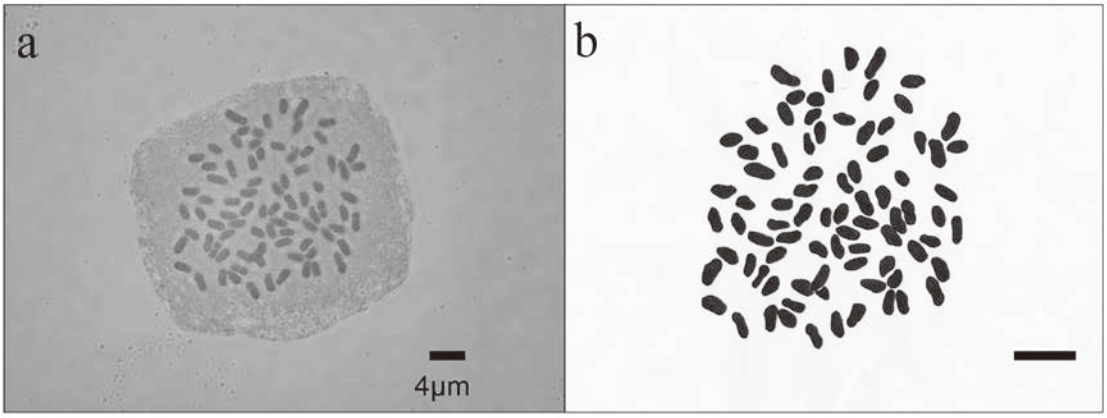


FIG. 2. Photograph (a) and illustration of a (b) of mitotic metaphase chromosomes of diploid sexual individual of *Dryopteris formosana* (*Hori 1409*). $2n = 82$.

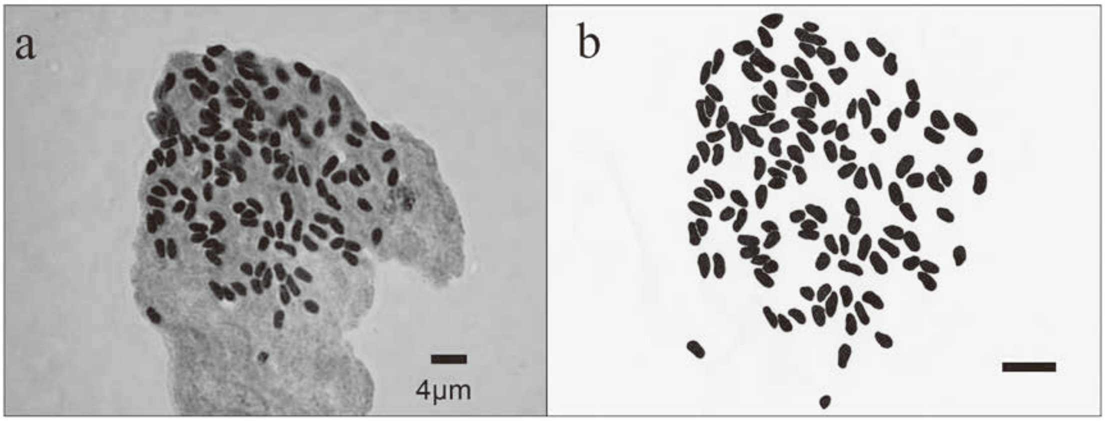


FIG.3. Photograph (a) and illustration of a (b) of mitotic metaphase chromosomes of triploid apogamous individual of *Dryopteris formosana* (*Hori 1412*). $2n = 123$.

spores per sporangium while 21 had 32 spores per sporangium (Appendix 1). For *D. varia*, 31 specimens had 64 spores per sporangium, whereas 20 specimens had 32 spores per sporangium (Appendix 2). They were therefore estimated to be sexual and apogamous cytotypes, respectively.

Based on the origin of the specimens, the geographical distribution of the sexual and apogamous types of *Dryopteris formosana* and *D. varia* in Twain were mapped (Fig. 4). Latitude and longitude could be estimated for only 33 and 49 localities of *D. formosana* and *D. varia*, respectively (Appendix 1, 2). Based on the localities, the elevation was evaluated for 20 and 23 of the collections of *D. formosana* and *D. varia*, respectively. The apogamous and sexual types of *D. formosana* were widely distributed in Taiwan. However, the sexual type of *D. formosana* was also distributed at lower elevations, 0–1,000 m (Fig. 5, p-value of f-test = 0.370, p-value of t-test = 0.031). The apogamous plants of *D. varia* were distributed over an elevation range similar to that of the conspecific sexual type (Fig. 6, p-value of f-test = 0.090, p-value of t-test = 0.288).

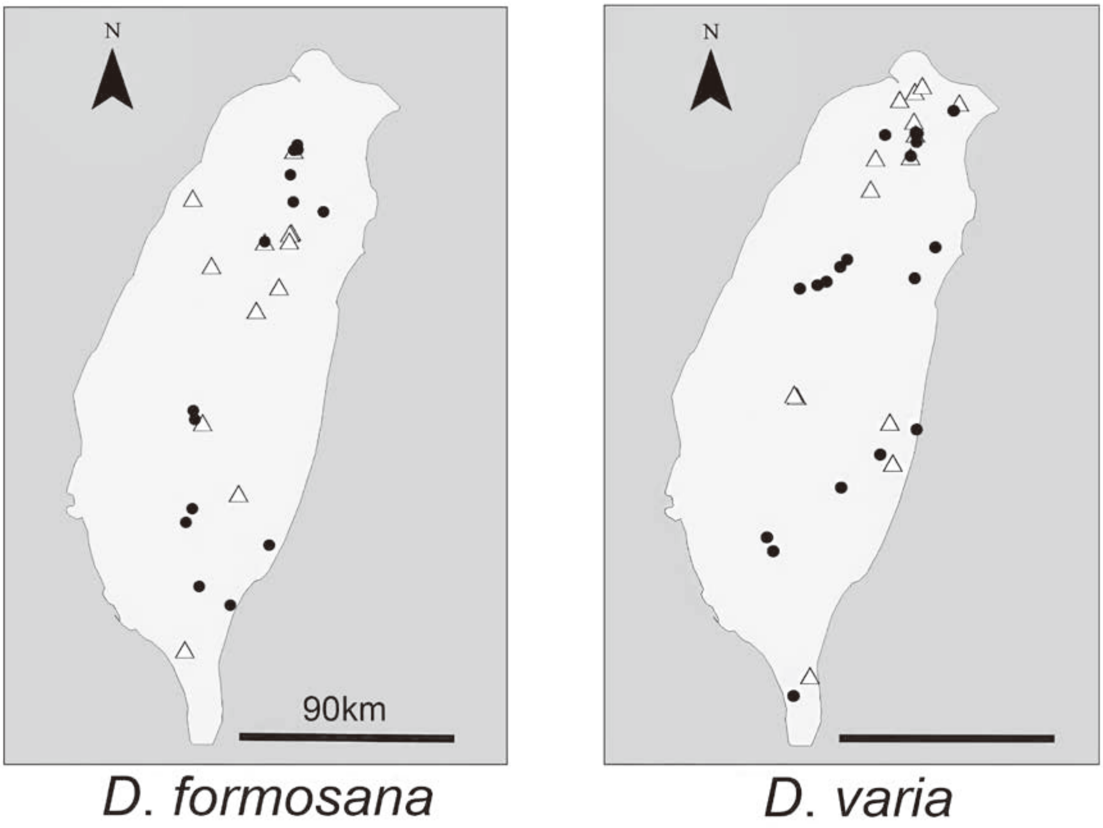


FIG. 4. Distribution of apogamous and sexual types of *Dryopteris formosana* (left) and *D. varia* (right) based on spore counts from herbarium specimens. Black circle, sexual type; white triangle, apogamous type. Scale bars = 90 km.

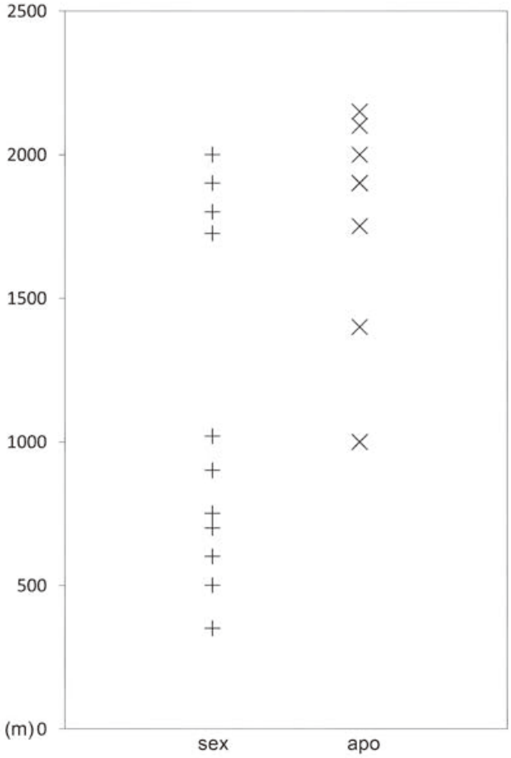


FIG.5. Scatter chart of reproductive mode and elevation in *Dryopteris formosana*.

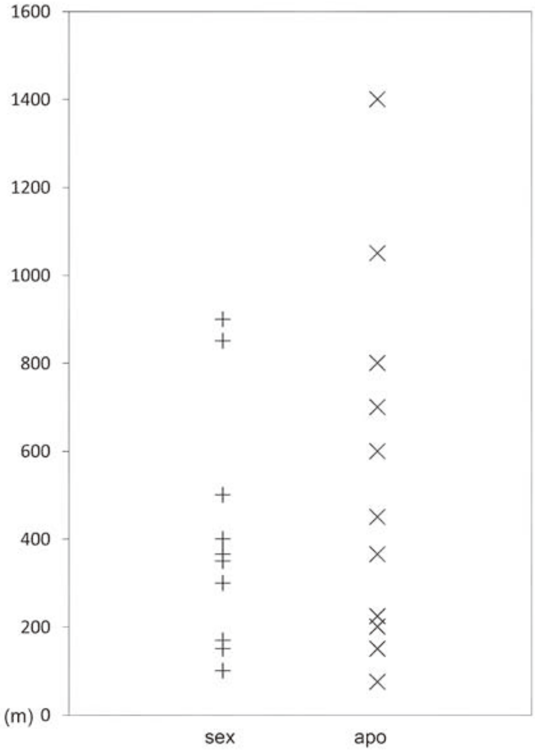


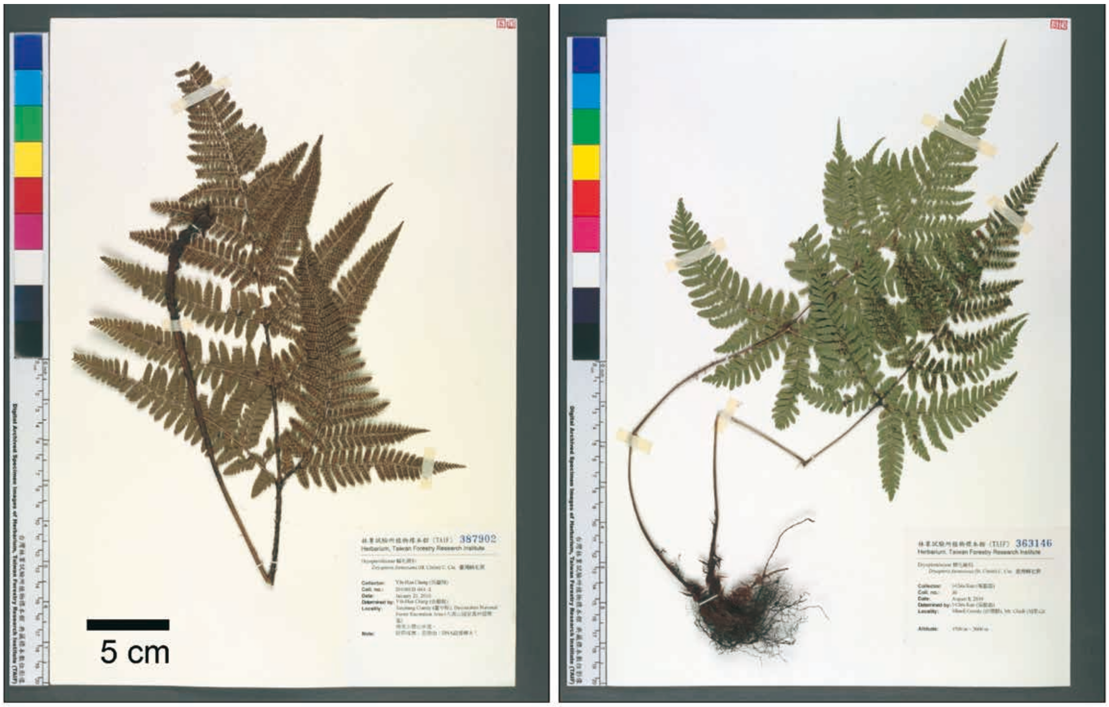
FIG.6. Scatter chart of reproductive mode and elevation in *Dryopteris varia*.

Discussion

Knowledge of the diploid sexual types are keys for understanding the origin of morphological and genetic variation in the apogamous species *of Dryopteris* subg. *Erythrovariae* sections *Erythrovariae* and *Variae*, because these two sections have been suggested to have experienced complicated reticulate evolution through hybridization between diploid sexual and diploid/triploid apogamous species/types (Lee & Park 2013, Hori *et al*. 2014). In fact, diploid sexual *D. varia* was shown to be involved in reticulate evolution in apogamous *D. pacifica* and *D. sacrosancta*, which are members of the *D. varia* complex (Lee & Park 2013, Hori *et al*. 2014).

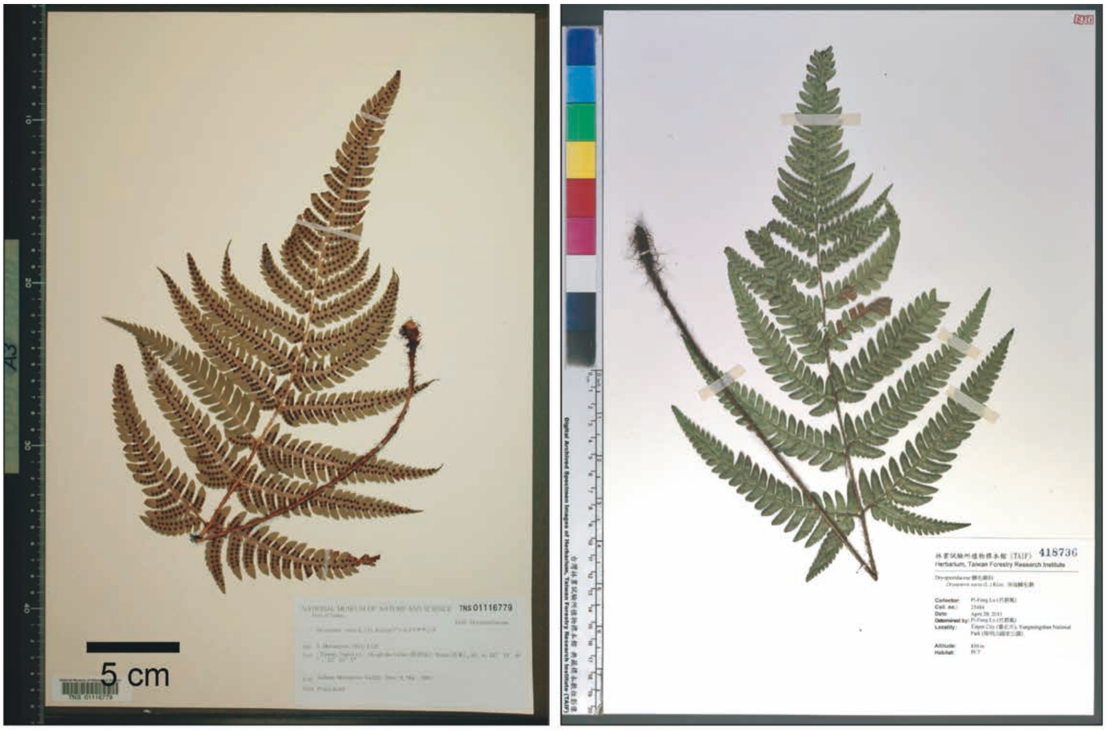
Triploid apogamous *Dryopteris formosana* and *D. varia* might be of autoploid origin because significant morphological differences between the apogamous and sexual cytotypes were not observed in either species (Fig. 7, 8).

In angiosperms, sexually reproducing cytotypes usually occur at lower elevations than their apogamous relatives (Bierzychudek 1985, Hörandl 2006). The sexual *Asplenium unilaterale* Lam. (Aspleniaceae) has also been reported to occur in more southern areas (Murakami & Iwatsuki 1983). The sexual diploid, *Pteris fauriei* Hieron. (Pteridaceae) occurs in warmer habitats than the apogamous triploid type (Huang *et. al*. 2007). *Dryopteris caudipinna* Nakai (a diploid sexual species) occurs in more southern areas than *D. erythrosora* (D.C. Eaton) Kuntze, which is a triploid apogamous species closely related to *D. caudipinna* (Yamamoto *et al*. 2010). Hori *et al*.



Sexual*(TAIF 387902)* Apogamous*(TAIF 363146)*

FIG.7. Gross morphology of sexual (*TAIF 387902*) and apogamous (*TAIF 363146*) *Dryopteris formosana* from Taiwan.



Sexual*(TNS 01116779)* Apogamous*(TAIF 418736)*

FIG.8. Gross morphology of sexual (*TNS 01116779*) and apogamous (*TAIF 418736*) *Dryopteris varia* from Taiwan.

(2015) demonstrated that sexual *D. chinensis* (Baker) Koidz. occurs in narrower, more southern areas than its apogamous relatives. However, there are a few exceptions as well. Tanaka *et al.* (2014) analyzed the elevation of various apogamous ferns in central Japan, and suggested that apogamous ferns become diminished at higher latitudes and elevations than sexual relatives. In the present study, sexual plants of *D. formosana* were found to be distributed at lower elevations than apogamous plants in Taiwan, whereas sexual and apogamous plants of *D. varia* were distributed over a similar elevations. Future research will require the identification of other environmental factors determining the distribution pattern of apogamous and sexual types of *D. varia*.

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APPENDIX 1. Specimens of *Dryopteris formosana* examined.

Reproductive mode	DNA amounts (pg.)	Chromosome numbers	Locality	Elevation	Date	Collector(s)	Collection no.	Herbarium no.		
								TAIF	TNS	MAK
sex	17.03	$2n=82$	Chiayi, Alishan	1900 m	Jul-1-2014	K. Hori	1394			423500
sex	16.97	$2n=82$	Chiayi, Alishan	1900 m	Jul-2-2014	K. Hori	1413			434051
sex	15.43	$2n=82$	Chiayi, Alishan	1900 m	Jul-2-2014	K. Hori	1414			434052
apo	24.9	$2n=123$	Nantou, Alishan, Tefuye historical Trail		Jul-2-2014	K. Hori	1412			434050
sex	17.07	$2n=82$	Taipei City, Mt. Chihtan	700 m	Jun-30-2014	K. Hori	1409			434048
sex			Taipei City, Mt. Chihtan	700 m	Jun-30-2014	K. Hori	1406			434046
sex			Taipei City, Mt. Chihtan	700 m	Jun-30-2014	K. Hori	1410			434049
apo			Nantou, Alishan, Tefuye historical Trail		Jul-1-2014	K. Hori	1397			423502
sex			Taoyuan, Tungyenshan	800–1000 m	May-30-2007	Yih-Han Chang	20070530-028	394573		
sex			Kaohsiung		Mar-17-1985	Bi-Jao Wang	4429	163605		
sex			Pingtung, Wutoushan		May-29-1996	Scheng-Zehn Yang	28539	150649		
sex			Hsinchu,Chienshih	1650–1800 m	Jul-26-2000	Ho-Ming H. Chang	3634	156358		
sex			Taitung, Taimali logging trail	600–900 m	Jul-1-2003	Shih-Wen Chung, Pei-Hsuan Lee	6564	190760		
sex			Taoyuan, Howei Giants Group		Dec-3-2011	Yih-Han Chang	20111203-028-2	400236		
sex			Taichung, Dasyueshan		Jan-21-2010	Yih-Han Chang	20100121-044-2	387902		
sex			Chiayi, Shihmeng Valley	1200–1800 m	Sep-16-2012	Pi-Fong Lu	24485	399081		
sex			Kaohsiung, Yuyushan	1700–1900 m	Mar-20-2001	Yih-Han Chang	3503	134651		
sex			Kaohsiung, Yuyushan	1700–1900 m	Mar-20-2001	Yih-Han Chang	3503	134653		
sex			Kaohsiung, Taoyuan		Sep-16-2001	Ming-Jer Jung	226	252976		
sex			Taoyuan, Xiao WuLai	1020m	May-4-2006	Ralf Knapp	s.n.	266740		
sex			Taitung, Tulanshan	500–700 m	May-8-2002	Shih-Wen Chung, Pei-Hsuan Lee	5448	165536		
sex			Taipei, Pichia Link Peak	200–500 m	Feb-17-2008	Pi-Fong Lu	15310	292211		
sex			Hsinchu, Kuanwu	2000 m	Jan-16-2002	Su-Wen Chung	5040	155483		
sex			Taipei, Wulai, Yunhsien Garden	500 m	Sep-28-1999	Pei-hsuan Lee	59	107501		
sex			Hudi Road		Aug-6-1968	T. Nakamura	1305		816092	
sex			Hudi Road		Aug-6-1968	T. Nakamura	1304		816093	
sex			Hudi Road		Aug-6-1968	T. Nakamura	1299		816098	
sex			Alishan		Jul-24-1970	T. Nakamura	111		816100	
sex			Alishan		Aug-25-1929	S. Sasaki	s.n.		197281	
apo			Ilan, Mt. Chung-yang-chien		Aug-27-1964	M. Tamura	s.n.		172212	
apo			Pingtung, Jinshui-ying, Chuenr Hsiang		Dec-6-2007	A. Ebihara	TW2006-144		762072	
apo			Taka		May-9-1960	H.Ageta	TKB38532		1038532	
apo			Taichung, Small Scared Tree Trail		Jan-19-2010	Yih-Han Chang	20100119-007	400217		
apo			Taoyuan, Howei Giants Group		Dec-3-2011	Yih-Han Chang	20111203-028-1	400235		
apo			Taichung, Ssuyuan	1900 m	Nov-22-2000	Her-long Chiang	1541	135838		
apo			Hsinchu, Kuanwu	2000–2300 m	Nov-27-1999	Pei-hsuan Lee	107	109218		
apo			Kaohsiung		Aug-25-1929	Ogami	s.n.	050935		
apo			Taipei, Palaka Road		Jul-3-2009	Yih-Han Chang	20090703-010	366798		
apo			Miaoli, Mt. Chiali	1500–2000 m	Aug-8-2010	I-Chia Kao	36	363146		
apo			Taitung, Wulu Logging Trail	1000 m	Mar-8-2009	Jinn-Fen Chen	s.n.	367222		
apo			Taichung, Mt. Tahsueh Logging Trail		Nov-25-2009	Yih-Han Chang	20091125-002	400296		
apo			Ilan, Ssuyuanyakaou	1800–2000 m	Jun-30-2012	Tian-Chuan Hsu	5930-2	392624		
apo			Ilan, Ssuyuanyakaou	1800–2000 m	Jun-30-2012	Tian-Chuan Hsu	5930-1	392625		
apo			Taitung, Wulu Logging Trail	1000 m	Mar-8-2009	Jinn-Fen Chen	s.n.	367221		
apo			Nantou, Huakang		Oct-7-2006	Zhi-Hao Chen	396	298097		
apo			Nantou, Huakang		Oct-7-2006	Zhi-Hao Chen	404	298096		
apo			Nantou, Huakang		Dec-17-2006	Zhi-Hao Chen	557	298093		
apo			Hualien, Sunghsuehlou		Nov-7-2001	Pei-hsuan Lee, Yih-Han Chang & Chai Ying Hu	1190	156201		
apo			Hsinchu, Kuanwu	2000 m	Aug-11-2000	Pi-Fong Lu	1467	149840		
apo			Taichung, 710 Logging Trail	2000–2200 m	Jul-7-2012	Tian-Chuan Hsu	5995-2	392704		

APPENDIX 2. Specimens of *Dryopteris varia* examined.

Reproductive mode	Locality	Elevation	Date	Collector (s)	Collection no.	Herbarium no.	
						TAIF	TNS
sex	Taichung, Pahsienshan		Nov-23-1922	S. Sasaki	*s.n.*	1193	
sex	Taipei, Sanhsia, Mt. Wuliaochienshan	500m	Dec-25-1999	H. M. Hunter Chang	2882	111024	
sex	Kaohsiung, Shihpalohanshan		Dec-14-1994	Y.C. Liou	5365	131390	
sex	Nantou, Huesuen		Mar-7-2001	Yih-Han Chang	3408	133530	
sex	Pingtung, Lilungshan		Jul-30-1999	Hung Ming-hui	751	142596	
sex	Taipei, Hunghoku	350m	Jul-14-2001	Ping-Hong Lu	587	145733	
sex	Taipei, Taipei City, Hsienchiyen	100m	Jul-14-2001	Ping-Fong Lu	602	145747	
sex	Taichung, Lileng Forest Load	700-1000m	Jul-30-2002	Her-long Chiang	2958	175251	
sex	Taitung, Tien-Lung suspension bridge	800-1000m	Oct-30-2003	Shih-Wen Chung	6784	195925	
sex	Pingtung, Woilososhan	300-500m	Aug-27-2004	Her-long Chiang	3742	216331	
sex	Taipei, Chiachiuliao	150m	Jun-2-2005	Wen-Fong Ho	2293	291334	
sex	Taichung, Lishan		Nov-24-2006	Zhi-Hao Chen	504	298109	
sex	Hualien, Nanan	250-350m	Nov-10-2012	Che-Wei Lin	24854	403518	
sex	Hualien, Cho-his Hsiang, Huang-ma	800-900m	Feb-22-1994	Yu-chuan Lu & Hsien-tsung Hung	1378	079760	
sex	Hualien, Hopingnanshi		Jan-3-1999	Tien-tsai Chen	9517	099683	
sex	Hualien, Hopingnanshi		Jan-3-1999	Tien-tsai Chen	9515	099773	
sex	Hualien, Xiulin		Aug-1970	T. Nakamura	1248		817348
sex	Hualien, Xiulin		Aug-1970	T. Nakamura	1249		817349
sex	Hualien, Xiulin		Aug-1970	T. Nakamura	1251		817350
sex	Hualien, Xiulin		Aug-1970	T. Nakamura	1250		817351
sex	Hualien, Xiulin		Aug-1970	T. Nakamura	1252		817352
sex	Taichung, Guguan		Apr-1-1972	A. Kosugi	*s.n.*		9536385
sex	Drow Bridge	366m	Nov-16-2003	Sadamu Matsumoto	Tw238		01104560
sex	Drow Bridge	366m	Nov-16-2003	Sadamu Matsumoto	Tw240		01104562
sex	Urai, Fushan	366m	Oct-19-2007	Sadamu Matsumoto	Tw789		01105153
sex	Urai, Fushan	366m	Oct-19-2007	Sadamu Matsumoto	Tw790		01105154
sex	Urai, Fushan	366m	Oct-19-2007	Sadamu Matsumoto	Tw792		01105156
sex	Urai, Hunghoku Valley		Mar-9-2003	Sadamu Matsumoto	Tw210		01116730
sex	Urai, Hunghoku Valley		Mar-9-2003	Sadamu Matsumoto	Tw209		01116777
sex	Urai, Hunghoku Valley		Mar-9-2003	Sadamu Matsumoto	Tw228		01116778
sex	Urai, Hunghoku Valley		Mar-9-2003	Sadamu Matsumoto	Tw229		01116779
apo	Taipei		Aug-1910	Kawakami & Shimada	*s.n.*	1194	
apo	Taipei, Chihtan	100-200m	Feb-18-2001	Her-long Chiang	1757	128907	
apo	Jinmen, Taiwushan		Jul-3-1997	Y.P. Yang	008600	141352	
apo	Taitung, Kuanghuanungchuang	200-250m	Aug-2-2001	Her-long Chiang	2642	145610	
apo	Hsinchu, Hsiuluan	800m	Sep-2-2002	Her-long Chiang	3079-2	180803	
apo	Taoyuan, Mt. Nachien	900-1200m	Jul-17-2003	Shih-Wen Chung, Jer-Hauer Lii, Chiao-Yu Kuo	6563	190414	
apo	Taipei, Shihfen Waterfall	50-100m	Sep-24-2003	Her-long Chiang	3426	212483	
apo	Taoyuan, Taman Bridge	600m	Apr-24-1987	Pi-Fong Lu	*s.n.*	270043	
apo	Nantou, Mt. Nengkao	2900m	Aug-26-2003	Yao-Mou Huang, Jun-Ming Chen	529	273721	
apo	Taichung, Lanhuachia		Sep-27-2007	Yao-Mou Huang	624	283265	
apo	Taipei, Chienshanhu Trail		Jun-20-2008	Yih-Han Chang	20080620-009	313249	
apo	Nantou, Shanlinhsi Forest		Aug-13-2000	Fay-Wei Li	FWL659-2	371104	
apo	Taipei, Yangmingshan National Park	450m	Apr-28-2013	Pi-Fong Lu	25484	418736	
apo	San-hsia, Mt. Yuan-shan	200m	Aug-23-1964	M. Tamura & H. Koyama	*s.n.*		245337
apo	Hualien, Hongye Wenquan		Mar-22-1972	T. Nakamura	*s.n.*		9536391
apo	Hulien, Anton		Mar-22-1972	S. Masuda	*s.n.*		9536415
apo	Urai, Fushan	366m	Oct-19-2007	Sadamu Matsumoto	Tw791		01105155
apo	Shanglinchi, Zhushan		Oct-21-2007	Sadamu Matsumoto	Tw848		01105221
apo	Urai, Hunghoku Valley		Mar-9-2003	Sadamu Matsumoto	Tw230		01116780
apo	Urai, Hunghoku Valley		Mar-9-2003	Sadamu Matsumoto	Tw231		01116781